SPORES FROM THE MIDDLE OLD RED SANDSTONE OF CROMARTY, SCOTLAND

by J. B. RICHARDSON

ABSTRACT. Plant spores are described from the Cromarty nodule beds (Middle Old Red Sandstone) of Scotland. The spores include three new genera *Cosmosporites*, *Rhabdosporites*, and *Ancyrospora*. The genus *Auroraspora* Hoffmeister, Staplin, and Malloy is emended to include forms, with a light coloured central body, which closely resemble spores of the species *Endosporites macromanifestus* Hacquebard. In agreement with Bhardwaj 1957 the genus *Cristatisporites* is here placed in the series Cingulati.

INTRODUCTION

THE principal fossils used as stratigraphic indices within the Middle Old Red Sandstone of Scotland are fossil fish; and a correlation based mainly on fish bands exists for this area. Recently, however, T. S. Westoll (1951) has suggested that the fish fauna of the main fish band (Achanarras band) may be a facies fauna because similar faunas are found at several levels on the south side of the Moray Firth. Westoll likewise indicates several anomalies in the fish fauna within the Orcadian basin. There is a need for evidence to supplement that provided by the fish remains and it is hoped that a study of the plant spores may eventually aid in elucidating the stratigraphic succession within the Old Red Sandstone basins.

Collections have been made of the fish bands from Orkney, Caithness, Cromarty, and from the south side of the Moray Firth and spores isolated from representative samples. The preservation of the carbonaceous material varies considerably in the different areas but it is excellent in the beds from the Cromarty area and has yielded an abundance of well-preserved spores some of which are described in this account.

Earlier work (Lang 1925) had drawn attention to the existence of a microflora in this region and contained descriptions and figures of nine types of plant spore identified under an arbitrary classification (A–I). During the present work Lang's earlier types have been recognized, together with a number of new types. The present account identifies and describes the new types of spores and revises some of the previously described spore types, bringing the whole together under a binomial system of classification for the first time in British Devonian microfloras. This will thereby facilitate subsequent identification of the microflora and enable more exact comparison with plant spores known from the Devonian of other areas. As the work proceeds it is hoped that a study of large numbers of these spores will enable limits to be set to specific variation, with the consequent evaluation of their stratigraphic usefulness. The assemblages so far studied correspond closely to assemblages known from the Middle Devonian of other areas particularly those from Europe and the U.S.S.R.

Acknowledgements. The author thanks Professor L. R. Moore for constant advice and encouragement throughout the work; and Professor P. C. Sylvester-Bradley for advice and useful discussion. Mr. R. Neves has read the manuscript and made several valuable suggestions. Thanks are due also to Mr. G. S. Bryant for help in producing the plate. The work forms part of a doctorate thesis of the University of Sheffield and was carried out under the supervision of Professor L. R. Moore during the tenure of a University of Sheffield Post Graduate Scholarship and a State supplemental award which are gratefully acknowledged.

[Palaeontology, Vol. 3, Part 1, 1960, pp. 45–63, pl. 14.]

Previous literature on Devonian plant spores. The earlier literature consists mainly of the incidental description and figures of spores associated with palaeobotanical work on fossil plants. Spores were obtained from sporangia by the use of cellulose film pulls and consequently the figures were often poor, and their descriptions too inadequate to enable comparisons to be made. As early as 1885 Clarke described 'spores' from Devonian deposits but Schopf (1957) commented, 'spore-like fossils may be present but some spherulitic and oolitic inorganic forms are evidently confused with them'.

Later more attention was paid to Devonian spores and they were isolated and described as distinct fossils. Lang (1925) described nine types of spores (A–I) from the Middle Old Red Sandstone of Scotland and later Krausel and Weyland (1929) described forms similar to Lang's types G and H from the Middle Devonian of Eberfield. These authors also described forms similar to, but smaller than, type G (Lang) from sporangia closely associated with the remains of *Aneurophyton germanicum.*

In 1936 Elovskava described seven spore forms from the Barzas coals (Kutznetsk basin, Russia) and classified these into groups and subgroups. In this work two main groups were instituted depending on the absence, or presence of 'wings', and referred to as groups 1 and 2 respectively. The 'wingless' spores of group 1 were further subdivided on the basis of ornamentation, size, and wall thickness, and those of group 2 were subdivided on width of 'wing' and ornamentation. Thomson (1940) used the same criteria to subdivide his Middle Devonian spores into seven groups as follows: 1 Laevigato—Zonales, 2 Apiculato—Zonales, 3 Angusto—Zonales (Magni), 4 Angusto—Zonales (Parvi), 5 Laevigati, 6 Granulati, and 7 Apiculati. Several of his forms resemble spores described by Lang as types A and C although type G, which is common in many Middle and Upper Devonian deposits, was not reported. Høeg (1942) followed Thomson's grouping and placed his seven types into Thomson's groups Granulati and Apiculati. The type F of Høeg (group Apiculati) is indistinguishable from some of Lang's type G and similar spores to type G (Lang) were also described from the *Archaeopteris* beds of Scaumenac bay, Canada (Arnold 1936).

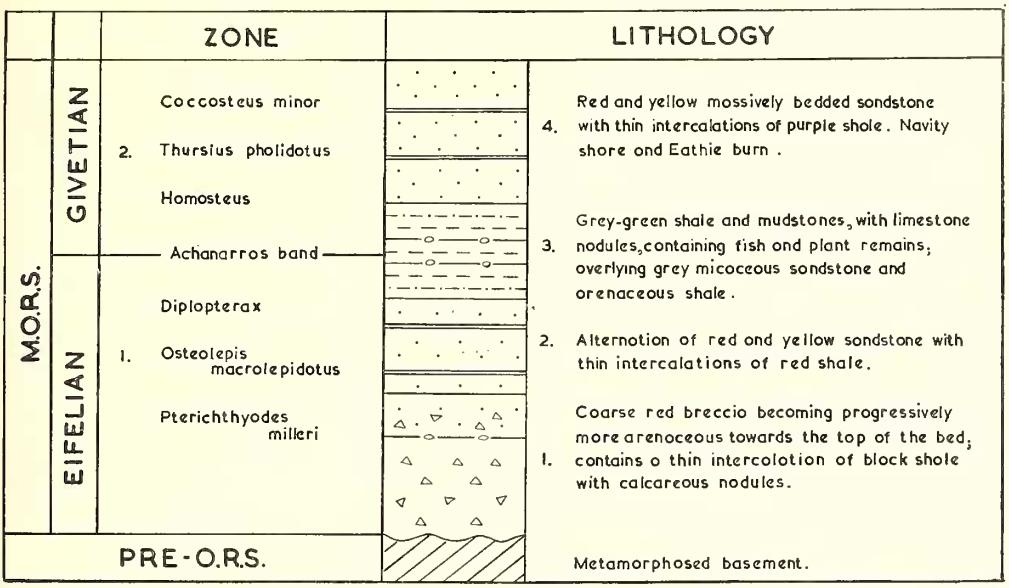
Eisenack (1944) described forms similar to types A, B, ?C, and G of Lang together with several new types, and utilized a system of binomial classification placing his forms into the genus *Triletes* Reinsch. Previously, however, Schopf (1938) had emended and restricted *Triletes* to a group of megaspores and, therefore, Eisenack's use of *Triletes* is not valid.

Recent workers have tended to use a binomial system of nomenclature, for example, Hoffmeister, Staplin, and Malloy (1955); Radforth and McGregor (1954), however, used an arbitrary system.

The most comprehensive work of Devonian spores is that of Naumova (1953) who described spores from the Upper Givetian, Frasnian, and Fammenian deposits of the U.S.S.R. In her classification (first proposed in 1937) Naumova used very wide subgroups and placed together forms which were structurally dissimilar. Further, although the figures are excellent, her descriptions are often inadequate. In view of these facts it is proposed to follow the classification of Potonié and Kremp (1954) which is widely used although not accepted without reserve.

Evidence of stratigraphic horizon. The Middle Old Red Sandstone age of the Orcadian deposits was established at an early date when Traquair, on palaeontological evidence,

substantiated the earlier view of Murchison. Traquair pointed out that three distinct fish faunas could be recognized in Scotland corresponding with Lower, Middle, and Upper Devonian. Further, the fossil fish have been used to zone the Middle Old Red Sandstone deposits of this area and, with the plant remains, have been used to equate the Orcadian deposits with Devonian sequences on the continent (Westoll 1951).



TEXT-FIG. 1. Succession of Middle Old Red Sandstone, Cromarty. (Fish zones based on Westoll 1937; 1951.)

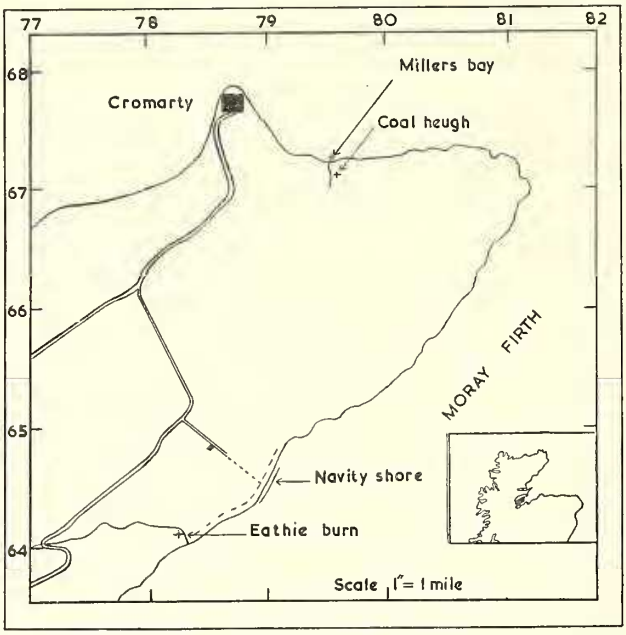
The Achanarras fish band, an important horizon in north-east Scotland, is traceable in Caithness, Orkney, Shetland, Edderton and Cromarty, and the south side of the Moray Firth. Westoll (1951) places the Achanarras horizon at the junction of the Eifelian and Givetian stages but refers to the possibility of the Achanarras fauna being a facies fauna although he says 'in general . . . this fauna seems to mark a narrow zone'.

The Cromarty fish beds are stated to yield a fauna comparable with that of the Achanarras fish band and are therefore probably Upper Eifelian to Lower Givetian in age.

Middle Old Red Sandstone deposits as developed in the Cromarty area and along the south side of the Moray Firth are much thinner (approximately 150–250 feet thick in the neighbourhood of Cromarty) than those in Caithness and Orkney. Furthermore, the lithology of the deposits is distinct in the two areas. The sequence in the Cromarty area is as seen in text-figure 1. All the Middle Old Red Sandstone strata shown in the section are probably very close to the junction of the Eifelian and Givetian.

Collections were made from the sequences at Miller's Bay, the Navity shore, and Eathie burn, and also from exposures at Coal Heugh. Spores have been isolated from samples of most of the rocks collected including the thin shale intercalation in the breccia (lithology 1, text-fig. 1) and the arenaceous shales of the Cromarty and Navity shores. The preservation of carbonaceous material is good in most of the beds but is excellent in the calcareous nodules and associated mudstones.

Method of preparation. Each sample was washed in distilled water and broken up into fragments about 5 mm. in diameter. It was then treated in dilute hydrochloric acid (1:5) and after all calcium carbonate had been removed, the acid was decanted and the material washed in distilled water. The residue was placed in a polythene flask and 40 per cent. hydrofluoric acid added. After it had been heated in a water bath for 16 to 24 hours



TEXT-FIG. 2. Index map of localities. Inset shows the Cromarty area (black) in relation to north Scotland.

the acid was decanted and the residue washed in distilled water. It was then treated in Schulze's solution for 2 to 3 hours, washed alternately in distilled water and potassium hydroxide, and finally mounted in glycerine jelly or canada balsam. Mounting in canada balsam was preceded by washing the material in successively more concentrated solutions of alcohol.

In the case of the shales bromine was used prior to heating in hydrofluoric acid. The fragments were soaked in bromine for 48 hours which broke the material down into a fine mud. It was then washed in distilled water until all the bromine was removed. The material was halved and subjected to either dilute hydrochloric acid (1:5) or dilute acetic acid (1:5) and then the residue was washed, treated with hydrofluoric acid, oxidized, and mounted as described above. Slides from the same sample treated with and without bromine and with hydrochloric or acetic acid show the spores to be comparable in size and relative abundance.

SYSTEMATIC DESCRIPTIONS

All the slides referred to by serial numbers in the text are in the collection of the Geology Department, University of Sheffield; position on the slide is indicated by the instrument settings of a Cooke, Troughton, and Simms microscope.

Order (Anteturma) POLLENITES R. Potonié 1931
Division (Turma) SACCITES Erdtman 1947
Subdivision (Subturma) MONOSACCITES (Chitaley 1951) Potonié and Kremp 1954
Series (Reihe) INTRORNATI Butterworth and Williams 1958
Genus AURORASPORA Hoffmeister, Staplin, and Malloy 1955

Type species *A. solisortus* H., S., and M. 1955

A group of monosaccate spores, without a limbus, which includes spores of type A (Lang) occurs regularly in all preparations. Besides type A (Lang) the group includes spores which closely resemble the species *Auroraspora solisortus* H., S., and M. In distinguishing *Auroraspora* from *Endosporites*, Hoffmeister, Staplin, and Malloy stated, '*Auroraspora* has a dark, subtriangular to subcircular central body and a delicate transparent bladder. . . . The central body of *Endosporites* approximates the bladder in thickness.' In the preparations studied by the author dark- and light-coloured central bodies occur in spores which are otherwise identical. Further, Hoffmeister, Staplin, and Malloy, in comparing *Auroraspora* and *Endosporites*, do not mention the limbus which is considered by many workers as a diagnostic feature of *Endosporites* and does not occur in *Auroraspora*. Therefore it appears desirable to emend *Auroraspora* so as to include all the spores of the monosaccate group described herein rather than to subdivide the group and erect a new genus for spores resembling type A Lang. It has not been possible to obtain cotypes of *Auroraspora solisortus* for this purpose.

Diagnosis. Radial, trilete, monosaccate spores, central body margin distinct; completely enclosed by a bladder which has no limbus and is unornamented.

Description. Colour, bladder pale to dark yellow, central body yellow to dark brown. Outline subtriangular with convex sides, to subcircular; central body subtriangular to subcircular in proximal view. Bladder completely encloses spore body, width of bladder around the central body (proximal view) equal to subequal; bladder has minute, often radiating, folds, or often strongly folded; may have strong folds along the tetrad rays, these folds usually reach the equatorial margin. Margin without limbus. Bladder externally smooth but infragranular or infrapunctate, infrapunctation often irregular; central body smooth. Length of tetrad rays varies from one-third to equal the radius of the body of the spore.

Comparison. This genus differs from *Endosporites* in the absence of a limbus. The spores of *Cosmosporites* gen. nov. (see p. 52) are very similar to those of *Auroraspora* but the spores of the former have an external ornament of cones or small spines and the presence or absence of ornament on these monosaccate spores is considered to be sufficient justification of generic distinction.

The spores of *Endosporites macromanifestus* Hacquebard have no limbus, and they appear to be identical to spores found in the Middle Old Red Sandstone of Scotland (Hacquebard 1957, p. 17) which are here placed in the genus *Auroraspora*. *E. macromanifestus* has a smaller size range (112–173 μ) than the spores described here (102–254 μ) and, therefore, the species is emended to include all the spores of the latter range.

Auroraspora macromanifestus (Hacquebard) emend.

Plate 14, figs. 1, 2; text-fig. 6A.

Type A Lang 1925, p. 255, pl. 1, figs. 1, 2.
Triletes velatus Eisenack 1944, p. 108 (pars) (not pl. 1, figs. 1–3).
Endosporites macromanifestus Hacquebard 1957, p. 317, pl. 3, figs. 14, 15.

Holotype. Hacquebard 1957, pl. 3, fig. 16; size 150 μ, central body diameter, measured from photograph, approximately 100 μ. Horton group (Mississippian), Nova Scotia.
Occurrence. Cromarty nodule beds (Achanarras horizon) Miller's Bay, Coal Heugh, Navity shore and Eathie burn; Lower Givetian, M.O.R.S.
Diagnosis. Spores radial, trilete; size 102 to 254 μ, body diameter 54 to 126 μ. Ratio of central body diameter to whole diameter 36 to 82 per cent. Outline dominantly subtriangular; spores have prominent folds along the tetrad mark, the folds reach, or nearly reach, the equatorial margin.

Description. Colour pale yellow to dark yellow, central body dark brown in some specimens. Equatorial outline subtriangular with convex sides and rounded apices. Central body round to subtriangular in proximal view. Bladder often folded and has pronounced folds along the tetrad marks, these folds usually reach the equatorial margin; bladder externally smooth but infragranular, or infrapunctate, infrapunctation irregular. Central body laevigate. Rays of the tetrad mark approximately half the radius of the body of the spore, only seen in a few specimens since commonly obscured by the triradiate folds.

Remarks. The size range of the specimens of *Auroraspora macromanifestus* found in shales associated with nodule beds on the Navity shore is greater than that for the spores isolated from these beds on the northern shore of Cromarty. Individual spores are larger than those found at Miller's Bay and Coal Heugh. The differences between spores from the two areas can be seen from the ratio of the body diameter to the whole diameter of the spore. The ratios for the three main localities are: Miller's Bay 50–73 per cent. (north shore, Cromarty), Coal Heugh 50–72 per cent. (north shore, Cromarty), Navity shore 36–82 per cent. (south shore, Cromarty). The range of the ratio for the spores of *A. macromanifestus* found on the Navity shore includes the range for this

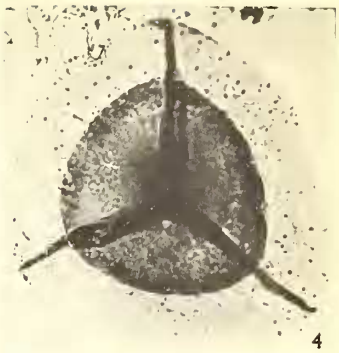
EXPLANATION OF PLATE 14

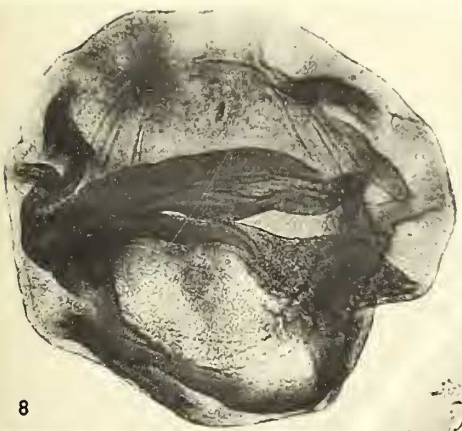
All figures magnified ×300 except where stated otherwise.

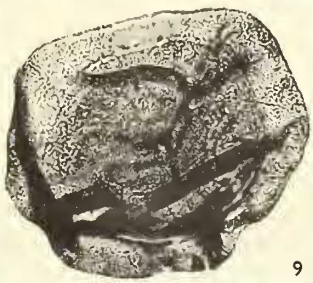
Figs. 1, 2. *Auroraspora macromanifestus* (Hacquebard). 1, slide CR. 155 reference 051559; 2, slide CR. 94. 184551 showing folding of the bladder.
Fig. 3. *Auroraspora aurora* sp. nov. Holotype, slide CR. 80 reference 188437.
Fig. 4. *Cosmosporites velatus* comb. nov. Slide CR. 170 reference 189631.
Figs. 5, 6. *Cosmosporites microspinosus* gen. et sp. nov. 5, holotype ×200, slide CR. 92 reference 195598. 6, ×600, part of the equatorial margin showing minute spines which bifurcate at their tips.
Fig. 7. *Ancyrospora grandispinosus* gen. et sp. nov. Holotype ×200, slide CR. 162 reference 156619.
Figs. 8–9. *Rhabdosporites langi* comb. nov. 8, slide CR. 61 reference 111465, large specimen showing pronounced folds. 9, slide CR. 47 reference 169624, small specimen showing triradiate mark.
Figs. 10, 11. *Densosporites devonicus* sp. nov. 10, holotype, slide CR. 80 reference 258499, showing folds along the triradiate mark. 11, spore showing triradiate mark, without folds.
Fig. 12. *Cristatisporites orcadensis* sp. nov. Holotype, CR. 81 reference 160471.
Fig. 13. *Cristatisporites conannulatus* sp. nov. Holotype, CR. 87 reference 140440.
Fig. 14. *Cristatisporites mediconus* sp. nov. Holotype, CR. 88 reference 093490.

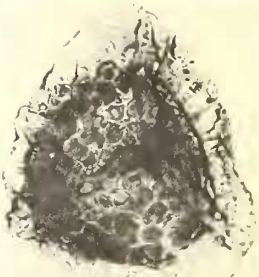

1

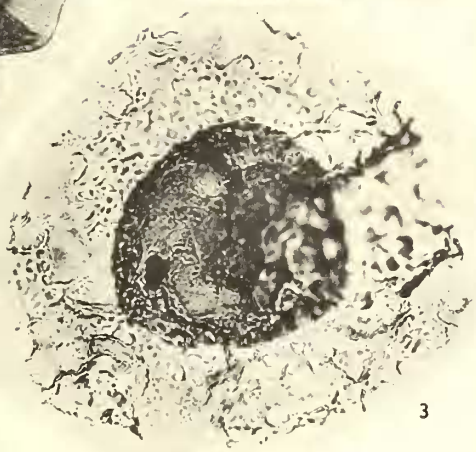

2

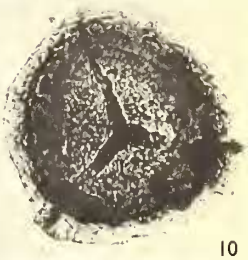

4

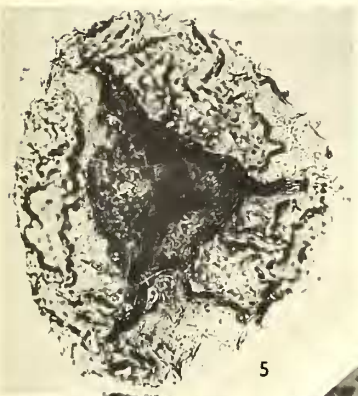

8

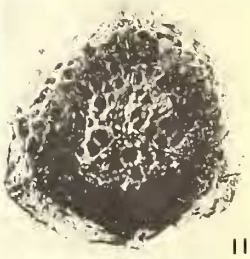

9

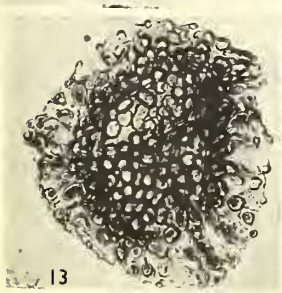

14


3

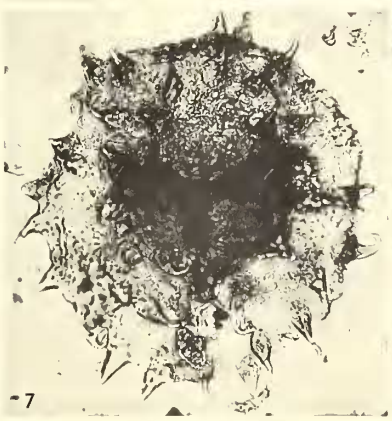

10

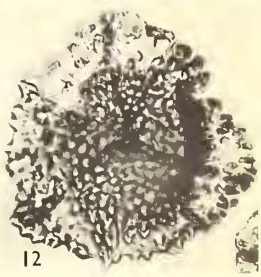

5


11


13


6


7


12

RICHARDSON, Middle Old Red Sandstone spores

species at the other two localities and, therefore, it is not considered justifiable separately to identify the larger spores.

These spores were originally described as type A by Lang (1925) and similar spores, from the upper Eifelian, were included in *Triletes velatus* by Eisenack (1944). Eisenack also included in this species forms which have a spinose ornament. In view of the heterogeneous nature of *T. velatus* and the fact that *Triletes* Reinsch was restricted to certain megaspores by Schopf in 1938, the species is not regarded as valid. Hacquebard (1957) described spores which appear to be identical with type A of Lang as *Endosporites macromanifestus*. The name *macromanifestus* is adopted here because, although *Triletes velatus* was erected in a prior publication, the spore chosen by Eisenack as the type of *T. velatus* has ornament (Eisenack 1944, pl. 1, fig. 2) and is referred to *Cosmosporites* (see below).

Auroraspora micromanifestus (Hacquebard) comb. nov.

Endosporites micromanifestus Hacquebard 1957, p. 317, pl. 3, fig. 16.

Holotype. Hacquebard 1957, pl. 3, fig. 16, size 88·6 μ, central body measured from photograph approximately 48 μ. Horton group (Mississippian), Nova Scotia.

This species is stated by Hacquebard to be identical to *Auroraspora* [*Endosporites*] *macromanifestus* except that it is smaller, and the bladder generally more distinctly infragranulose. It is, therefore, included here in the genus *Auroraspora*.

Auroraspora aurora sp. nov.

Plate 14, fig. 3

Holotype. Size 201 μ, body diameter 108 μ. Slide CR. 80. Reference 188437. Shales from the Cromarty nodule beds, Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, Coal Heugh, Navity shore and Eathie burn; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 120 to 201 μ, body diameter 66 to 108 μ. Ratio central body diameter to whole diameter 35 to 60 per cent. Outline rounded to subtriangular, bladder very thin and with minute folds.

Description. Colour yellow to dark yellow, central body brown in some specimens. Equatorial outline subtriangular with convex sides, or rounded. Central body round to subtriangular in proximal view. Width of bladder around the central body equal to subequal. Junction between central body and bladder distinct. Bladder thin, often wrinkled into numerous small folds. Bladder and body laevigate. Folds along the tetrad mark are absent. Triradiate mark usually distinct, rays of the mark vary from one-third to one-half and occasionally equal the radius of the body of the spore.

Comparison. A. aurora differs from *A. macromanifestus* in the rounded or rounded triangular outline of the spore and the central body. The bladder in *A. aurora* is often very fine and is wrinkled into numerous small, often radiating, folds. The spores do not possess the prominent folds along the tetrad mark which are typical of *A. macromanifestus*. In *A. aurora* the rays of the tetrad mark vary a great deal, from one-third to equal the radius of the body of the spore.

There is a close resemblance between *A. aurora* and *A. solisortus* H., S., and M., and the difference is one of size. The species *A. solisortus* has a range of 61–78 μ compared with a range of 120–201 μ in the species *A. aurora*.

Series (Reihe) EXTRORNATI Butterworth and Williams 1958

Genus COSMOSPORITES gen. nov.

Type species *Cosmosporites velatus* (Eisenack) comb. nov.

Diagnosis. Radial, trilete, monosaccate spores, completely enclosed in a bladder which has no limbus. Equatorial outline subtriangular with convex sides; central body round to subtriangular. Spores originally elliptical in polar section. Bladder has an external ornament which consists of pointed cones or spines which usually bifurcate at their tips. Folds often present along the rays of the tetrad mark. Derivation of name: G. Cosmos, ornament.

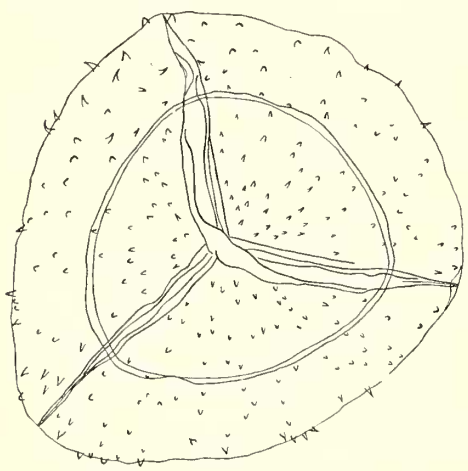
Comparison. This genus is erected for what appears to be a homogeneous group of spores which possess an external ornament of cones or short spines. It is distinguished from *Grandispora* H., S., and M. by its marked subtriangular outline, the possession in some of the spores of small spines which bifurcate at their tips, and by its large size.

Cosmosporites velatus (Eisenack) comb. nov.

Plate 14, fig. 4; text-fig. 3

Triletes velatus Eisenack 1944, p. 108 (pars), pl. 1, figs. 1–3.

Holotype. Eisenack 1944, pl. 1, fig. 2; size 208 μ, central body 114 μ, cones 1 μ. Probably Middle Devonian.



TEXT-FIG. 3. *Cosmosporites velatus* comb. nov. Camera lucida drawing $\times 500$.

Occurrence. Cromarty nodule beds (Achanarras horizon), Coal Heugh, Miller's Bay, Navity shore, Eathie burn; especially abundant at Coal Heugh; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 108 to 208 μ, body 54 to 116 μ; bladder has an external ornament consisting of cones of variable size in different spores, cones 1–4 μ.

Description. Colour of the bladder pale yellow, body dark yellow to brown. Equatorial outline subtriangular with convex sides and rounded apices, body rounded to sub-triangular. Bladder ornamented by pointed cones of variable size on different spores, usually between 1 and 2 μ, occasionally they are 4 μ long. Ornament appears to be confined to the distal surface. Body distinct smooth. Bladder is sometimes strongly folded and there are folds along the triradiate mark which reach the equatorial margin. Triradiate mark, often obscured by folds, two-thirds of the radius of the body.

Comparison. Cosmosporites velatus differs from *C. microspinosus* sp. nov. by its ornament of cones, the larger central body in relation to the whole diameter, and by its smaller size.

Cosmosporites microspinosus sp. nov.

Plate 14, figs. 5, 6

Holotype. Size 249 μ, central body 100 μ. Slide CR. 92. Reference 198598. Cromarty fish band (Achanarras horizon), Navity shore.

Occurrence. Shales at the tops of the Cromarty nodule beds on the Navity shore, shales at Coal Heugh (Achanarras horizon); Lower Givetian, M.O.R.S. Rare.

Diagnosis. Spores radial, trilete; size 186 to 282 μ, central body 98 to 156 μ; bladder has an external ornament consisting of minute spines which usually bifurcate at their tips and are widely spaced, spines 3 to 9 μ long.

Description. Colour yellow to dark yellow, central body brown. Equatorial outline subtriangular with convex sides and rounded apices, body triangular to subtriangular. Width of bladder around central body subequal. Ornament consists of minute spines which usually bifurcate at their tips, are widely spaced, and are borne on the distal surface and the equatorial margin. Central body indistinct, appears smooth. Bladder often folded and corroded. Prominent folds obscure the tetrad mark and usually reach the equatorial margin.

Remarks. Eisenack (1944) in his description of *Triletes velatus* records that he has spores which have small bifurcating spines, and these may be comparable to *C. microspinosus* sp. nov. Eisenack, however, did not figure or name these spores but considered that they were intermediate between his species *Triletes velatus* and *T. paravelatus*. In the material studied, however, the spores which resemble *T. velatus* have a loose exine which is demonstrated by folding which does not affect the central body, whilst spores which resemble *Triletes paravelatus* (probably *Cristatisporites*) are also found, but in these spores the exoexine and the intexine appear to be attached as no folding has been observed which affects only the exoexine (text-fig. 8).

Genus RHABDOSPORITES gen. nov.

Type species *Rhabdosporites langi* (Eisenack) comb. nov.

Diagnosis. Radial, trilete, monosaccate spores completely enclosed in a bladder which has no limbus. Equatorial outline of both bladder and body subcircular to elliptical. Spores originally spherical, or nearly so, with body attached on the proximal side. Bladder possesses an external ornament which covers the whole surface and consists of evenly distributed, closely packed rods which are parallel sided elements and have truncated tips. Body membrane smooth. Derivation of name: G. Rhabdo, rod.

Comparison. The nature of the external ornament distinguishes this genus from *Glomospora* and *Remysporites* Butterworth and Williams which also possess an external ornament. In contrast to the evenly distributed rods of *Rhabdosporites*, *Glomospora* has an external ornament consisting of 'slightly raised spiral or parallel ridges', and in *Remysporites* the bladder is laevigate to microreticulate.

Rhabdosporites langi (Eisenack) comb. nov.

Plate 14, figs. 8–9; text-figs. 4, 6в

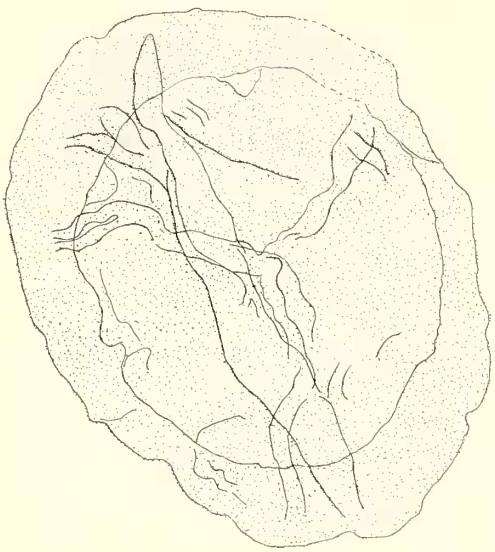
Type B Lang 1925, p. 256, pl. 1, figs. 3–6.
Triletes langi Eisenack 1944, p. 112, pl. 2, fig. 4.

Holotype. Eisenack 1944, pl. 2, fig. 4; size 174μ, central body 132μ. Probably Middle Devonian.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, Coal Heugh, Navity shore, and Eathie burn; especially abundant at Coal Heugh; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 95μ to 190μ, central body 67 to 154μ; bladder covered with fine rods, 0·5 to 1μ long.

Description. Colour of the bladder yellow, central body yellow to brown. Equatorial outline of both the bladder and the central body, subcircular to elliptical; central body often placed eccentrically. Bladder is ornamented, uniformly covered by densely packed rods which are parallel sided and have truncated tips. Central body smooth. Bladder usually strongly folded. Triradiate mark often indistinct, rays one-half to one-third, and occasionally nearly equal to, the radius of the body of the spore; sometimes there are folds on the bladder parallel to the rays of the trilete mark.



TEXT-FIG. 4. *Rhabdosporites langi* comb. nov. Camera lucida drawing ×500.

Remarks. Lang (1925) figured *Rhabdosporites* as type B and later Elovskava (1936) included spores of similar appearance in group 2 form 5. In form 5 Elovskava included spores with and without ornamentation and described them as having a wing which was one or two layered. One of Elovskava's figures (pl. 3, fig. 1), however, is ornamented, has folds, and resembles *Rhabdosporites*.

Naumova (1953) figured spores as *Archaeozonotriletes* which appear to resemble *Rhabdosporites*. *Archaeozonotriletes* as defined by Naumova appears to be a very heterogenous group and probably includes spores which have a bladder and others with a cingulum. Of Naumova's species, *Archaeozonotriletes macromanifestus* most closely resembles *Rhabdosporites* as far as can be determined from Naumova's drawings and descriptions but *A. macromanifestus* has a definite narrow equatorial rim which is not present in *Rhabdosporites*. Further it is not certain whether or not *A. macromanifestus* has a bladder and Naumova did not mention any folding which is a common feature of *Rhabdosporites*. Potonié (1958), in emending *Archaeozonotriletes*, drew attention to its heterogeneous nature as defined by Naumova. He took *A. variabilis* as type species and proposed to include in the genus only forms which are similar to it. Potonié stated that *A. variabilis* has an eccentric cingulum but Naumova's drawings indicate that it may have a bladder. The species *A. variabilis*, in contrast to *Rhabdosporites*, has a smooth surface.

Genus ANCYROSPORA gen. nov.

Type species *Ancyrospora grandispinosa* sp. nov.

Diagnosis. Radial, trilete, monosaccate spores, completely enclosed in a bladder without a limbus. Equatorial outline circular to subcircular, body subcircular to subtriangular. Spores originally elliptical in polar section; central body attached on proximal and distal surfaces. Bladder bears large processes which bifurcate at their tips. Derivation of name: G. Ankyra, anchor.

Comparison. Ancyrospora differs from *Grandispora* H., S., and M. in the presence of large anchor-shaped appendages and in the large size of it spores. It differs from *Cosmosporites* in having circular to subcircular outline in equatorial view, large spines and thick exine. *Hystricosporites* McGregor 1960 also has grapnel-shaped appendages but has no central body.

Remarks. The term bladder is used here because, although in *Ancyrospora* it is a thick membrane which bears large spines, it is in part widely separated from the central body. Naumova used the term perispore, but, since her interpretation of this feature differs from that used by Potonié and Kremp (1955, p. 19), adoption of this term would only lead to confusion. The author regards the outer layer of this spore as the exoexine and the central body as the intexine. Further, the perisporal membrane occurs on the spores of modern plants, it is not usually preserved in the fossil state, and it has a structure which is very different from that of the exoexine and the intexine.

Ancyrospora grandispinosa sp. nov.

Plate 14, fig. 7; text-figs. 5, 6c

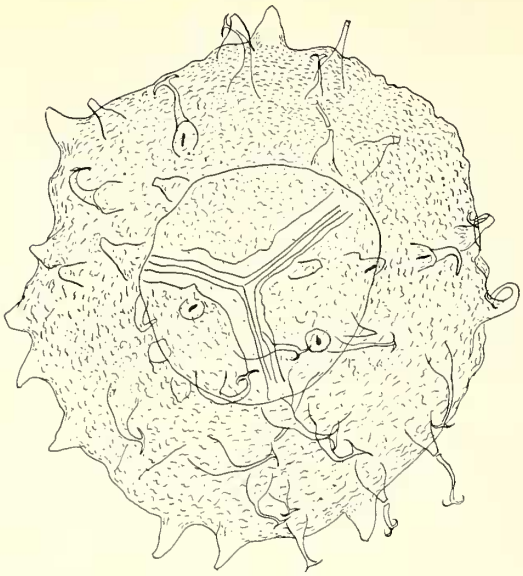
Holotype. Size 237 μ, central body 114 μ; spines 39 to 51 μ. Slide CR. 162. Reference 158617. Cromarty nodule beds. Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Navity shore, Coal Heugh, and Eathie burn; Lower Givetian, M.O.R.S.

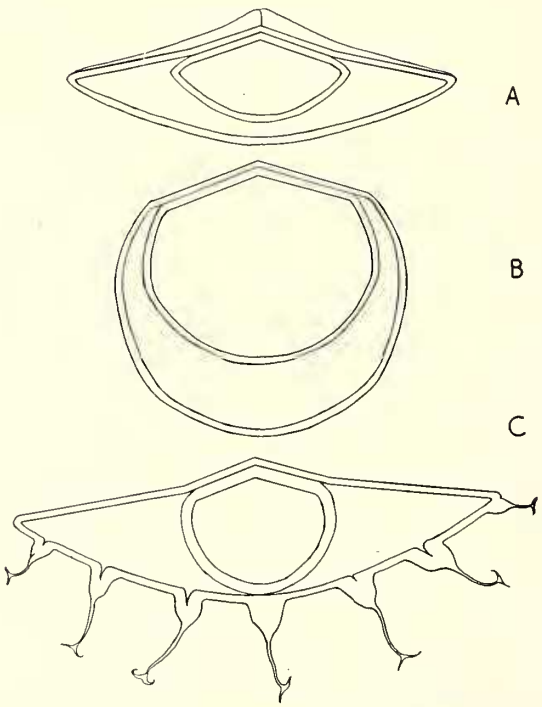
Diagnosis. Radial, trilete, spores; size 174 to 276 μ, body diameter 90 to 210 μ; outline circular to subcircular; bladder bears spines which have wide bases and bifurcate at their tips, 24 to 54 μ long.

Description. Colour dark yellow to dark brown. Equatorial outline of the bladder and body circular to subcircular. Body occasionally subtriangular. Bladder width around the central body equal to subequal in proximal view; surface of the bladder covered by numerous minute wrinkles; infrapunctate; central body smooth. Bladder bears long spines with hollow, wide, conical bases which taper sharply to a more slender stem, the stem tapers more gently to the apex where it swells slightly and bifurcates, the tips of the spines are pointed; spines 24 to 54 μ long, 9 to 54 μ apart. Triradiate mark distinct, with raised lips, equal to the radius of the body of the spore.

Comparison. This species resembles *Archaeotriletes houestus* Naumova 1953 (horizon Fammenian) except that around the central area of Naumova's spores there is a thickened zone and the size is 90 to 100 μ, considerably smaller than the smallest specimen of *Ancyrospora grandispinosa* (174 μ). *Archaeotriletes* has been emended by Potonié (1958) and now includes only spores with a membranous zona. Type G 1 of Lang is identical to some spores included in *A. grandispinosa.*



TEXT-FIG. 5. *Ancyrospora grandispinosa* gen. et sp. nov. Camera lucida drawing × 300.



TEXT-FIG. 6. Diagrammatic reconstructions in polar section. A, *Auroraspora macromanifestus*. B, *Rhabdosporites langi*. C, *Ancyrospora grandispinosa*.

Order (Anteturma) SPORITES H. Potonié 1893
Division (Turma) TRILETES Reinsch 1881
Subdivision (Subturma) ZONOTRILETES Waltz 1935
Series (Infraturma) CINGULATI Potonié and Klaus 1954
Genus DENSOSPORITES (Berry 1937) Potonié and Kremp 1954

Type species *Densosporites covensis* Berry 1937

Densosporites devonicus sp. nov.

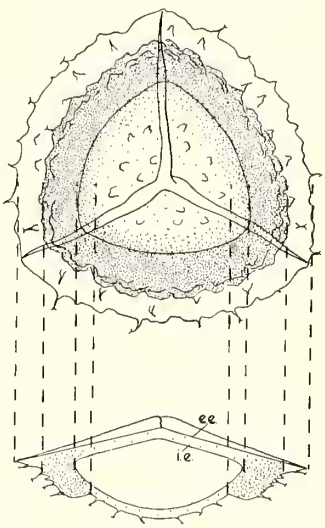
Plate 14, figs. 10, 11; text-fig. 7

Holotype. Size 110μ, cingulum 27–33μ; Slide CR. 80. Reference 127511. Shales at the top of the Cromarty fish band (Achanarras horizon), Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon) only found in samples from the shales associated with the nodule bed, Navity shore; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 87–159μ, cingulum 18–39μ; dark and light zones of the cingulum clearly separated, dark zone greater than, or equal to, width of light zone; distal surface and equatorial margin ornamented with spines which often bifurcate at their tips; rays of tetrad mark one-half to two-thirds and occasionally equal radius, often accompanied by folds to equatorial margin.

Description. Colour pale yellow except for the inner zone of the cingulum which is dark brown and often opaque. Equatorial outline subcircular to subtriangular in proximal view. Dark and light zones of the cingulum distinct, dark (inner) zone overlaps the central area, the outer edge of this zone is more irregular and has the form of a series of overlapping scales; outer light zone is thin membranous often with a scalloped margin. Ornament consists of distinct spines which cover the distal surface and equatorial margin; they vary a great deal in thickness, length, and density, and vary from types in which the bifurcation is barely perceptible to ones in which it is well developed with the extremities considerably splayed. Exine infrapunctate, especially marked on the central area. Rays of the tetrad mark one-half to two-thirds and occasionally equal the radius of the spore, folds often run parallel to them and reach the equatorial margin. The folds are wider in the polar region than at the equatorial border.



TEXT-FIG. 7. *Densosporites devonicus* sp. nov. Diagrammatic reconstruction in plan view and polar section; e.e., exoexine; i.e., intexine.

Comparison. This species is distinguished from other species of *Densosporites* by the large size, and presence of spines which bifurcate at their tips and by the frequent occurrence of prominent folds along the tetrad mark. *Hymenozonotriletes inaequus* McGregor (1960) has more prominent spines which do not bifurcate but have papillate tips.

Remarks. Potonié (1958) has emended *Hymenozonotriletes* Naumova and selected *H. polyacanthus* Naum. as type species. Naumova's figures of this spore (1953, pl. 4, figs. 11–12) show a zone of equatorial thickening, prominent triradiate folds, and also relatively

long spines. Structurally *Hymenozonotriletes* (Naum.) Potonié appears to be very similar to *Densosporites* and, in emending *Hymenozonotriletes*, Potonié stated, 'the zona resolves itself more or less into longer rays' (presumably the equatorial spines). 'In this fact appears to exist a distinction to certain forms of the genus *Densosporites*' (Potonié 1958, p. 29). This distinguishes *Densosporites* and *Hymenozonotriletes* on the degree of development of the spinose ornament. In the author's opinion this is an insufficient basis for generic distinction since it would be difficult to name spores with intermediate spinose development. The spores described here have not the prominent spinose development of *Hymenozonotriletes* and therefore are placed in *Densosporites*.

With regard to the structure of *Densosporites* it may be important that in some spores included in the genus there are folds along the triradiate mark which reach the equatorial margin (Potonié and Kremp 1956, text-fig. 51 and pl. 18, figs. 390, 405–7). The prominent folds along the triradiate mark in *Densosporites devonicus* are regarded by the author to indicate a continuous membrane on the proximal surface (see text-fig. 7). Bhardwaj (1957), discussing the same feature in comparing *Lycospora* and *Cirratriradites*, stated that he did not consider it important that in certain species of *Lycospora* the triradiate folds do not cross the equatorial flange, whereas in *Cirratriradiate* the folds extend across the flange to the equatorial margin. He stated: 'If the cingulum is part of the trilete apparatus, i.e. modification of the arcuate ridges, the trilete rays must extend on to it as in *Cirratriradites*.'

In view of the fact that there is doubt as to the importance of the continuous tetrad marks, that species with such marks are included in *Densosporites*, and that the valid publication of *Hymenozonotriletes* is later than that of *Densosporites*, the spores described here are placed in the latter genus.

Genus CRISTATISPORITES Potonié and Kremp 1955

Type species *Cristatisporites indignabundus* (Loose) Potonié and Kremp

Remarks. A group of spores found closely resemble *Cristatisporites* Potonié and Kremp. Three species are recognized in this group as follows, *C. orcadensis*, *C. conannulatus*, and *C. mediconus*. Most of the spores of the three species show a clear differentiation into a central area and an equatorial flange (text-fig. 6) and therefore the genus *Cristatisporites* is here included in the subdivision Zonotriletes. In one of the species described below, *C. conannulatus*, the cones around the margin of the central area are fused giving rise to a thickened band, and in another species, *C. orcadensis*, there are some spores which have a flange completely covered by cones making it a very stout structure. Both these structures are in contrast with the more or less membranous collar or corona of fused hairs, which form the flat strongly spreading structure of series Zonati (Potonié and Kremp 1954); therefore the spores described here are placed in the series Cingulati. This is in agreement with Bhardwaj (1957), who placed *Cristatisporites* in the Cingulati. After studying the diplotype and several species of *Cristatisporites* he concluded that it was closely related in structure and organization to *Densosporites*.

Cristatisporites orcadensis sp. nov.

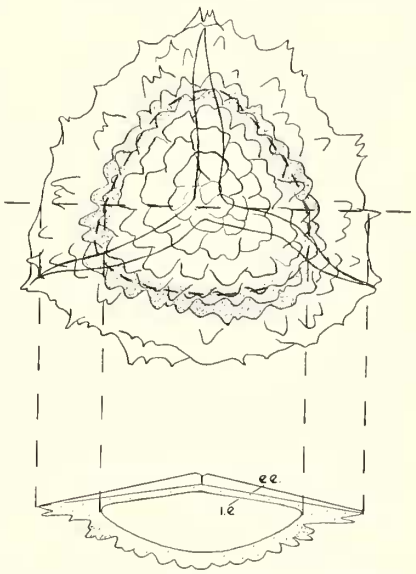
Plate 14, fig. 12; text-fig. 8

Holotype. Size 112 μ, central area 72 μ. Number of peripheral cones 46. Slide Cr. 81. Reference 160471. Cromarty nodule beds (Achanarras horizon).

Occurrence. Cromarty nodule beds (Achanarras horizon), Coal Heugh, Navity shore, and Eathie burn; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 96–153 μ in diameter, central area 63–102 μ; ratio of central area diameter to whole diameter 57 to 98 per cent. Cones on central area and flange rounded to pointed, large number of peripheral cones up to 49, sharply pointed giving a dentate margin; cones 3–7 μ wide, 4–9 μ high.

Description. Colour yellow to dark yellow. Subtriangular in equatorial outline with convex sides and rounded apices. There is a differentiation to form a central area and flange which in some specimens is distinct while in others it is hidden by the ornament. Ornament, distal, consists of cones which occur on the central area and the flange. Cones on the central area vary; in some spores they form concentric patterns and are fused at their bases, whereas in others they are fused in groups and are less regular. Some cones are larger and closely packed and possess polygonal bases. Cones on the central area have pointed or rounded apices whilst those on the flange have mainly pointed apices, are less regularly distributed, and occasionally form groups; cones on the central area width equal to or greater than, height, cones on flange height often greater than the base. Marginal cones sharply pointed, often in groups of two or three cones, give denticulate margin, in some specimens they become very long and form an incised border. Number of cones around equatorial margin twenty to forty-nine. There are prominent triradiate folds which obscure the tetrad mark and which usually reach the equatorial margin.



TEXT-FIG. 8. *Cristatisporites orcadensis* sp. nov. Diagrammatic reconstruction in plan view and polar section; e.e., exoexine; i.e., intexine.

Comparison. Some of the spores included in *C. orcadensis* resemble the figure of *Hymenozonotriletes praetervisus* Naumova 1953 (Upper Givetian, Russian Platform) but the description of the latter is insufficient to allow detailed comparison and further *H. praetervisus* is smaller than *C. orcadensis*. *Hymenozonotriletes* Naum. is defined to include all forms with a thin filmy margin (Naumova 1937) and appears to include spores with a bladder as well as spores with a flange or cingulum.

Cristatisporites orcadensis differs from both *C. conannulatus* and *C. mediconus* by the presence of numerous pointed cones on the central area and zona, and the large pointed cones on the equatorial margin.

Eisenack (1944) figured and described *Triletes paravelatus* which probably belongs to *Cristatisporites*. Eisenack's photographs are not very clear but they show differences to *C. orcadensis*. The latter has well-marked flanges along the triradiate mark which are not shown in the figures of *T. paravelatus*, the size range is smaller than that of *T. paravelatus*, and the outline is more regular.

Cristatisporites conannulatus sp. nov.

Plate 14, fig. 13

Holotype. Size 112 μ, central area 72 μ. Number of peripheral cones twenty-four. Slide CR. 87. Reference 140439. Shales at the top of the Cromarty fish band (Achanarras horizon), Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, and Navity shore; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete; size 99 to 120 μ, central area 69 to 96 μ, ratio of body diameter to whole diameter 57 to 98 per cent. Large rounded cones, fused in groups, on central area and flange, and fused in a ring around the margin of the central area; cones 6–9 μ wide, height less than width.

Description. Colour yellow to dark yellow. Spores radial, trilete, subtriangular in equatorial outline. Ornament distal, consists of large rounded cones, height less than width. Near the junction of the central area and the equatorial flange the cones are fused to form a continuous ring which simulates a thickened band. Cones on the centre of this area more scattered, and fused in small groups of two or three; cones on the flange are widely spaced, also rounded and are fused in groups. The equatorial cones vary from ten to thirty-four in number, smaller than the others, are mainly rounded but occasional pointed cones are also present. Prominent triradiate folds obscure the tetrad mark and reach the equatorial margin. These folds are broader at the proximal pole than at the equatorial margin.

Comparison. This species differs from *C. orcadensis* and *C. mediconus* in the rounded nature of the cones on the central area and flange and their fusion around the margin of the central area in the form of a ring.

Cristatisporites mediconus sp. nov.

Plate 14, fig. 14

Holotype. Size 120 μ, central area 78 μ, flange 12 to 22 μ. Peripheral cones small, twelve in number. Slide CR. 88. Reference 092490. Shales at top of the Cromarty nodule beds (Achanarras horizon), Navity shore.

Occurrence. Cromarty nodule beds (Achanarras horizon), Miller's Bay, and Navity shore; Lower Givetian, M.O.R.S.

Diagnosis. Spores radial, trilete, size 90–135 μ, central area 70–93 μ, ratio of central area diameter to whole diameter 53 to 83 per cent., consists of large rounded cones confined to the central area, width 6–18 μ; height 3–6 μ, and few small peripheral cones.

Description. Colour yellow with dark yellow to dark brown central area. Outline subtriangular with convex sides and rounded apices. Central area sharply divided from a well defined flange 12 to 27 μ wide. Ornament is on the distal surface, consists of large rounded cones restricted to the central area and a few small cones on the equatorial margin. Cones of the central body are rounded, closely packed, and show a polygonal pattern at their bases. The height of the cones is less than, or equal to, the width; equatorial margin bears only a few small pointed cones five to twenty-two in number. There are prominent triradiate folds which obscure the tetrad mark and reach the equatorial margin; the folds are wider at the proximal pole than at the equatorial margin.

Comparison. This species is distinguished from *C. conamulatus* and *C. orcadensis* by the large cones on the central body and the general lack of cones on the flange with few, small and pointed cones on the equatorial margin.

CONCLUSIONS

Two distinctive features of the Middle Old Red Sandstone spores are seen: (*a*) the large size of many of the spores and (*b*) the predominance of spores which have spinose appendages terminated by grapnel-tipped hooks.

With regard to the size, Naumova mentioned that the Givetian spores she studied were represented for the most part by large forms. Of the spores described in this paper five species range over 200 μ as follows: *Auroraspora aurora* (120–210), *A. macromanifestus* (102–254), *Cosmosporites microspinosus* (186–282), *C. velatus* (108–208), *Ancyrospora grandispinosa* (174–274), and *Rhabdosporites langi* nearly reaches 200 μ (95–190).

With regard to the type of spore the entire assemblage is very distinctive, especially so in view of the predominance of Type G of Lang. These spores are characterized by long spinose appendages which bifurcate at their tips. Since Lang described type G in 1925 spores from various parts of the world, with similar spinose appendages, have been referred to it. Although the appendages are similar, however, the group defined on the basis of this specialized ornament is probably heterogeneous, as other features of these spores vary greatly and differ from those originally defined as type G. More work needs to be done before the spores arbitrarily described as type G can be fitted into the binominal classification.

The spores with anchor-shaped processes, as pointed out by Naumova, resemble the massulae of the modern water fern *Azolla*. It is possible that the similar appendages of type G spores served to facilitate attachment and may have helped the spore to float (in *Azolla* the hooks aid the attachment of macrosporangial and microsporangial massulae). Further, the fact that the spores have thick walls also suggests that water was the medium of transport. It is perhaps significant that spores with these two features are so predominant in the Devonian.

Spores with an ornament of grapnel-tipped processes, as seen in type G (Lang), have not been recorded from the Carboniferous and this appears to be a feature peculiar to Devonian spores. However, in addition to this type of organization there are spores with bladders, cingulae, and zonae (e.g. *Auroraspora*, *Rhabdosporites*, *Densosporites*, and *Cristatisporites*), all of which types of organization are well known in the Carboniferous. In the Middle Old Red Sandstone it is notable that the particular spinose ornamentation referred to may be present upon spores which otherwise simulate the organization of Carboniferous spores (e.g. *Densosporites devonicus* and *Cosmosporites microspinosus*).

Finally, the assemblage of plant spores found in north-east Scotland is comparable with those assemblages described from other Middle Devonian deposits by Eisenack, Krausel and Weyland, Naumova, and Thomson. The significance of spores of type G can be judged from the fact that they have been observed in North America, Spitzbergen, Germany, and Russia in deposits of Middle and Upper Devonian age. The assemblage found in the Middle Old Red Sandstone deposits of Scotland corresponds, in general, with that described by Naumova (1953) from the Upper Givetian of U.S.S.R. but since